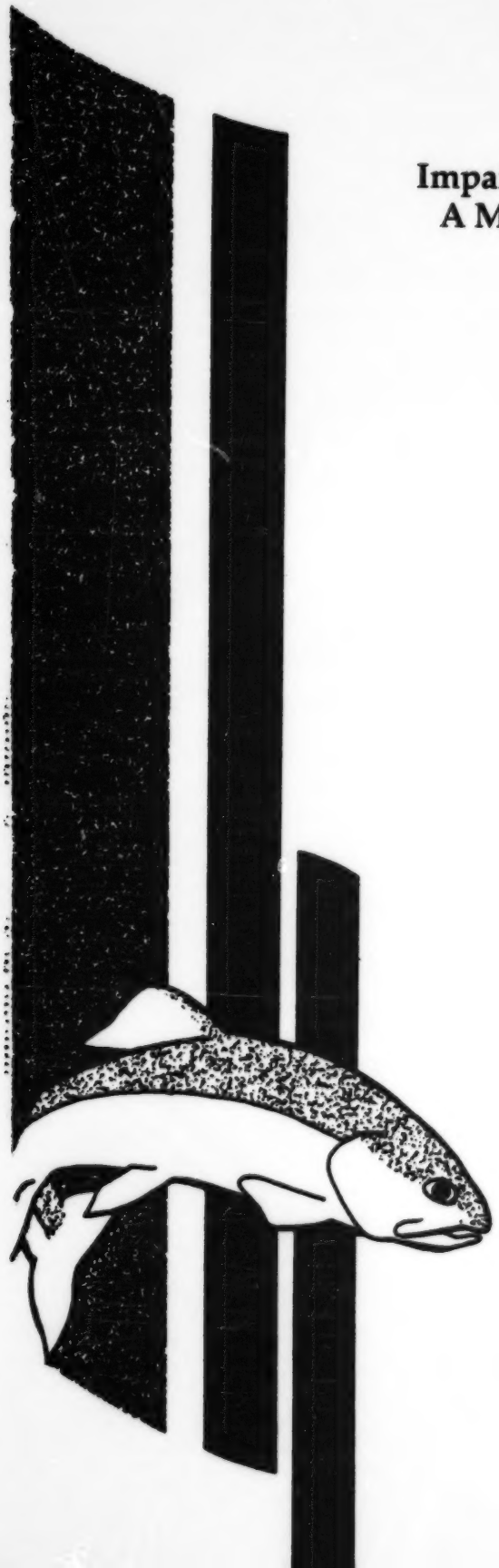

Impaired School Formation at Low Density: A Mechanism for Depensatory Mortality in Sockeye Salmon

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ABSTRACT

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A simple encounter model was used to simulate the process of school formation at dawn for different densities of juvenile sockeye salmon. The results suggest that the process of school formation may be severely inhibited by a low encounter rate among juvenile sockeye at the lowest densities commonly observed in natural populations. Encounter rates of predators with schools are insensitive to density because, under a given set of conditions, asymptotic school density is similar over a wide range of initial densities of prey individuals. Enhanced school formation may reduce predation risk at high sockeye density and provide a mechanism for the multiple equilibrium hypothesis of sockeye dominance cycles.

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INTRODUCTION

During the lacustrine phase of their life history sockeye salmon are planktivores that commonly school in the deeper, darker areas of the pelagic zone during the day (Eggers 1978), vertically migrate upward to feed at dusk (Levy 1987) and then descend at dawn. Both schooling (Godin 1986) and vertical migration (Clark and Levy 1988) are presumably predator defense mechanisms. Schools generally break up at dusk and reform again at dawn (Levy 1989). In the process of reforming schools each morning, sockeye face the problem of finding each other and forming a school before encountering a predator. At the same time, they may try to take advantage of low dawn light levels to feed during an "anti-predation window" (Clark and Levy 1988) before spending the day, not feeding, but in the relative safety of a school in deep water at very low light levels. Given a constant density of predators, the problem of school formation should be more severe at lower densities since sockeye are having more and more difficulty finding each other while encountering approximately the same number of predators.

There are two situations in which sockeye can vary tremendously in density but appear to face a relatively constant predator density. In some lakes, sockeye exhibit cyclic dominance and the densities of juveniles can vary by almost 2 orders of magnitude during the 4 year period of the cycle (Williams et al. in press). The most important predators (rainbow trout, lake trout, burbot) are relatively long lived (4-10+ years) and only a few leave the lake as adults for brief spawning and feeding excursions. Non-anadromous sockeye (kokanee) adults are also planktivores in the pelagic zone of deep lakes and may face a similar problem, particularly in situations where they coexist with populations of anadromous sockeye. Kokanee outgrow some of their predators as age-1 and age-2 fish, but the densities of these older fish is much lower and they may have difficulty forming schools of similar sized/aged fish, particularly in situations where most of the age-0 population leaves the lake as age-1 smolts. In addition, any sudden decline in a kokanee population may be reinforced by impaired schooling since declines in relatively long lived predators should lag behind those of their prey.

In this paper, a simple encounter model will be used to illustrate the schooling problem and to provide some quantitative predictions to test the model. The schooling problem will also be discussed in the context of the more general problem of depensatory predation and the role of predators in driving sockeye cycles and kokanee population fluctuations. Although there are possible advantages to schooling behaviour in addition to predator protection (Pitcher 1986), a basic assumption in this analysis is that schooling confers an antipredator benefit which reduces predation risk (Godin 1986, Major 1978).

A second assumption is that sockeye are unable to maintain schools at night rather than simply not choosing to do so. Some marine fishes are able to maintain schools under amazingly low light conditions (Glass et al. 1986) but as is the case with gear avoidance (Glass and Wardle 1989) bioluminescence may be an important factor in the marine environment. Although light is considered to be the main sense involved in schooling, other cues such as the lateral line, sound and smell could also be used. Under truly dark conditions, however, many fish do not appear use these other senses to compensate for a lack of vision (Glass et al. 1986). Many commercially caught marine fish do not react to the approach of large, noisy trawls which, even under dim light, consistently generate various escape behaviours (Glass and Wardle 1989). Sockeye do not appear to feed on dark nights (Doble and Eggers 1978) although they may school under bright moonlight (Levy 1989). Estimates of visual acuity in sockeye (Ali 1959), suggest schooling is possible at the surface on starlit nights but that visual schooling at depth on a cloudy night would not be possible.

THE MODEL

The probability of both prey-prey encounters and predator-prey encounters was estimated using the mean velocity model of Gerritsen and Strickler (1977). In this model, encounter probabilities depend on 6 parameters: N_H, the density of prey schools, N_p, the predator density, u, the swimming velocity of the prey, v, the swimming velocity of the predator, R_H, the encounter radius of one prey for another, and R_p, the encounter radius of the predator for a prey. R_p is typically large enough that predators encounter schools (or individuals when school size equals one) rather than individuals within a school. N_H therefore represents the density of schools (number of schools per unit volume) and declines as schools form. The effects of non-circular visual fields (Dunbrack and Dill 1984) and the finite thickness of the fish layer are ignored.

Assuming that v>u, the probability of a prey encounter per unit time for each predator (Gerritsen and Strickler 1977, equation 6) is:

$$Z_p = (\pi R_p^2 N_H) * (u^2/v + 3v) / 3 \qquad (1)$$

Similarly, the probability a prey will encounter another prey individual in a unit of time is:

$$Z_H = 4\pi R_H^2 N_H u / 3 \qquad (2)$$

since in this case u=v and $R_H=R_p$. Substituting N_p for N_H in (1), the probability that a prey will encounter a predator in a unit of time is:

$$Z_{HP} = (\pi R_p^2 N_p) * (u^2/v + 3v) / 3 \qquad (3)$$

The ratio of prey-prey to prey-predator encounters (E_R), both for a prey individual, and in a unit volume of water, is:

$$E_R = Z_K/Z_{HP} = 4N_H R_H^2 u / (N_p R_p^2 (u^2/v + 3v)) \qquad (4)$$

A non-circular visual field should have little effect on the general conclusions if the shape does not change with increasing encounter radius. The net effect of a finite thickness for the fish layer is that the exponents of R_H and R_p will decline to a limit of 1 when the layer is very thin and R_H and R_p are large. Encounter rates for large encounter radii are therefore overestimated but the problem is not easy to deal with since the edges of the layer are poorly defined.

Model Parameters

The theoretical population used in this study resembles the sockeye/kokanee population in Shuswap Lake, which has a pronounced dominance cycle, long-lived, resident predators (rainbow trout, lake trout, burbot) and no significant pelagic planktivore competitors (Williams et al. in press).

The range of prey densities covers the approximate range of densities of dominant and off year populations of underyearling sockeye in Shuswap Lake, B. C. (100 fish/hectare to 5000 fish/hectare). Densities of adult (age-2, age-3) kokanee in four B.C. lakes are much lower (10-100 fish/hectare, data on file). Area densities were converted to volume densities using the approximate thickness (10 m) of the dense portion of typical morning sockeye layers (Levy 1989). Predator densities are unknown and therefore only encounters per predator are estimated.

Swimming velocities are assumed to be in the energetically efficient range of 1-3 body lengths/sec (Ware 1978) which agrees with measured search velocities of cutthroat trout and dolly varden char (Henderson and Northcote 1985). Prey (age-0 and age-2 Oncorhynchus nerka) are assumed to be 7 and 20 cm in length and have constant search velocities of 14 and 40 cm/sec, respectively (ie. two body lengths/s). Predators are assumed to be 50 cm in length and have a search velocity of 100 cm/s.

Encounter radii can also be approximately defined. R_H and R_p are assumed to be equal and results are presented for a range of a common radius, R_E. An estimate of the approximate maximum

values of the reactive distance can be made using estimates of measurements of reactive distances for much smaller objects. Under dawn light intensities, reactive distances of both cutthroat trout and dolly varden char to 1.5 mm Diaptomus is about 5-10 cm (Henderson and Northcote 1985). A 70 mm sockeye would subtend the same angle at a distance of 2.4-4.6 m. Ware (1973) indicates that reactive distance increases at less than a proportional rate with prey size. At longer distances, light attenuation also becomes a significant factor in reducing reactive distance. Vertical light extinction coefficients in Quesnel Lake, for example, (Levy 1989) indicate that light intensity is halved in about 3.5 m.

R_E is assumed to increase rapidly with time to an asymptotic value, R_A,:

$$R_E = .3R_A t/(2+.3t) \qquad (5)$$

where t is time (min). R_E equals $.5R_A$ in about 6.7 minutes. Varying this rate of increase had little effect on the qualitative results of the model.

The process of school formation can conceivably effect most of the parameters in the model. For schooled fish, many eyes may see predators sooner, raising R_H, or more secure fish may be less vigilant, lowering R_H. Schooled fish may swim slower to avoid predator contact or faster to feed. Larger schools may be visible at longer distances, raising both R_H and R_P.

In the iterative version of the model, N_H is used to represent the density of schools and is therefore equal to the initial density divided by the current school size. Every prey-prey encounter is assumed to result in coalescence into a bigger school. Search velocities do not change as school formation proceeds. Time steps are 1 second.

The only other adjustment as schools increase in size is that R_E is assumed to increase. The increase in R_E results from the assumption that vision is limited because prey blend into the background but that prey individuals on the edge of the school are encountered before the center of the school. In this case:

$$R_T = R_E + R_S \qquad (6)$$

where R_S is the radius for the average school and R_T is the current encounter radius for both predators and prey. Schools are assumed to be spherical with a diameter determined by spherical close packing with an average separation of one body length (Van Olst and Hunter 1970). The non spherical nature of small schools can be ignored for $R_E >> R_S$.

An alternative assumption that prey detection is limited by the angle subtended by an object results in much more dramatic increases in R_T with school size since R_T would be a multiplicative function of R_E and R_S:

$$R_T = 2R_E R_S / L_H \qquad (7)$$

where L_H is the prey length. The angle subtended is important for nearby, high-contrast objects in clear water but turbidity reduces reactive distance (Vinyard and O'Brien 1976) and light attenuation should therefore be an overriding factor in detecting cryptic objects at distances where light attenuation is important.

Additional assumptions concerning the number of prey captured per encounter as a function of school size are needed to translate encounter rates into mortality rates. I limit the model to encounters only since captures/encounter are often low (Vermeij 1982) and can rise, fall or stay the same as school size increases (Godin 1986).

RESULTS

If encounter radii, swimming velocities and the density of predators are constant as prey density rises, then the number of prey-prey encounters rises faster than the number of predator-prey encounters (Equation 4). More intuitively, at a low prey density, each prey individual has a low probability of encountering another prey before encountering a predator. At a high prey density, each prey has a high probability of encountering another prey, and forming a protective school, before encountering a predator even though each predator is also encountering more prey at higher densities. Considerations such as predator handling time and predator satiation reinforce this trend. The actual values of encounter radii of schooled and unschooled prey do not affect this conclusion.

Equation (4) also suggests some strategies that prey could employ to increase the rate of schooling relative to the rate of predator encounter. Small increases in R_H relative to R_P would have a large effect since E_R is proportional to $(R_H/R_P)^2$. Since E_R is proportional to $u/(u^2/v+3v)$, increases u relative to v would have much less of an effect than changes in encounter radii.

An iterative model can be used to illustrate these general results. As prey density increases, encounters per predator increase (Fig. 1a), but school size also increases (Fig. 1b). Individual prey have a similar probability of encountering a predator at all densities but at high densities prey encounter each other more frequently and form large schools in which they are presumably (eg. Godin 1986, Major 1978) less vulnerable on an

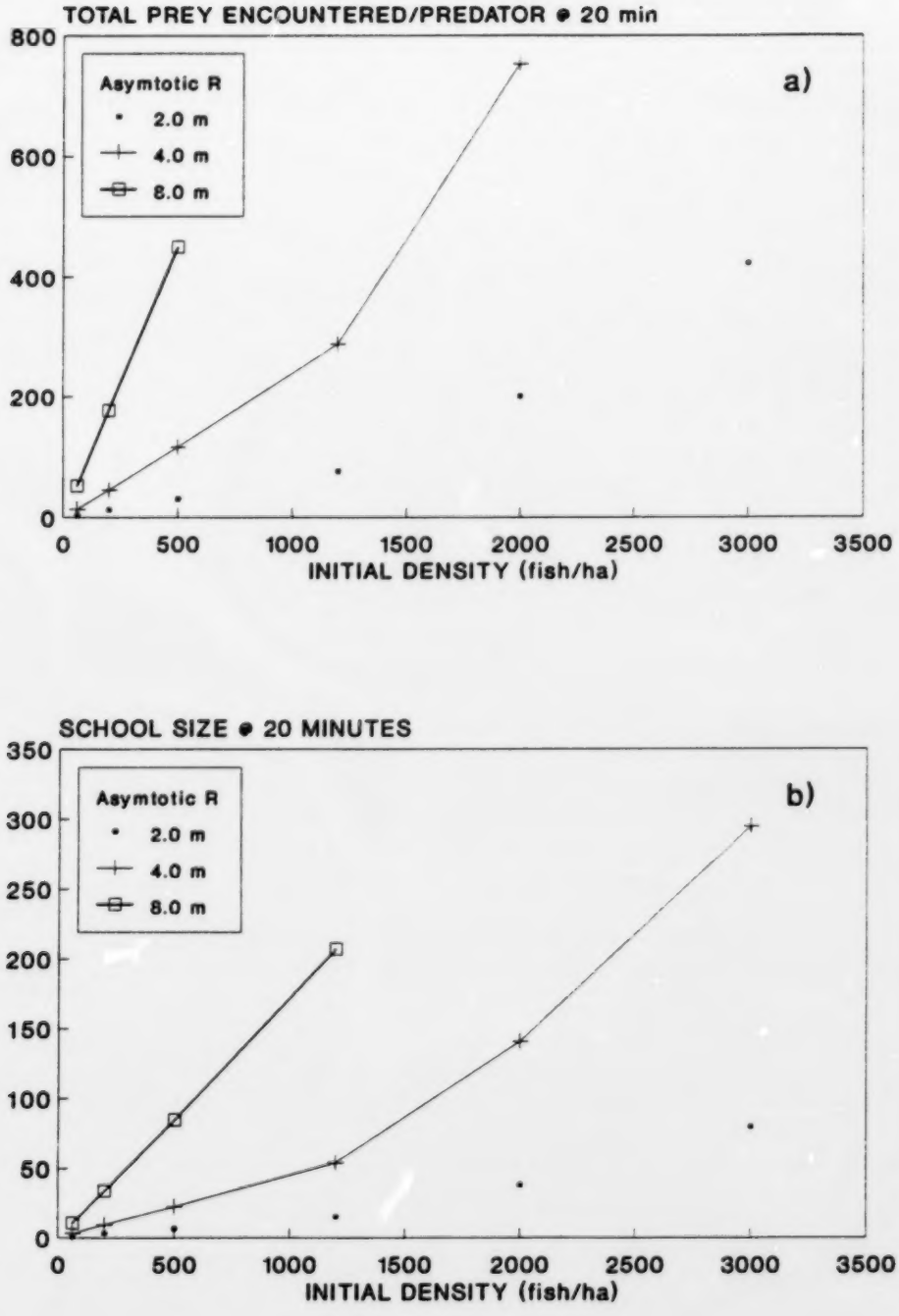

Fig. 1. (a) Total number of prey encountered by each predator during the first 20 minutes following the initiation of school formation versus initial prey density and (b) average school size versus initial prey density at 20 minutes after the initiation of school formation. Values were produced by the iterative encounter model described in the text.

individual basis. Thus the ultimate value of the school is a reduction in the probability of capture upon encounter rather than a reduction in an individual prey's probability of encountering a predator. The upward curvature of the lines (Fig. 1) is caused by the increase in encounter radius with school size.

Actual estimates of the rate of school formation are very sensitive to R_H, but at the lowest extreme of prey density, the rate of school formation is slow even for very high values of R_H (Fig. 2a). At the more reasonable value of R_A = 2.0 m, it takes approximately 30 min. to reach an average school size of two at a density of 60 prey/hectare).

The iterative model also indicates that school density, and therefore the encounter rate of predators with schools, rapidly converges on a common value for a wide range of individual densities, especially if the encounter radius is high (Fig. 2b). This suggests that predators would have only a short time each morning to take advantage of high prey densities unless they repeatedly attack large schools. The convergence on a common density of schools rather than a common school size also implies that school size will be approximately proportional to density throughout the day. Larger schools formed at higher density have a larger encounter radius which raises encounter rates and reinforces this trend.

For 20cm kokanee, schools form more rapidly than for 7cm sockeye at 60 fish/hectare but at low kokanee densities (15 fish/hectare) school formation is again slow (Fig. 3).

DISCUSSION

Pitcher and Turner (1986) and Helfman (1986) have suggested that piscivore activity is high at twilight (eg. Major 1977) because piscivores are able to approach their prey more closely at this time. For schooling prey species at low densities, the time taken to form a school each morning may also represent an opportunity that is exploited by piscivores since schools appear to perform an antipredator function in a variety of species (Godin 1986). The problem is much less serious at dusk since schools are generally disbanding at this time.

Analytical and verbal models of low density, pelagic prey populations suggest that school formation at dawn always works better as an antipredator strategy at higher prey densities. For a given R, N_p, u and v, the encounters that prey have with predators always less dangerous at higher density if we assume that increasing school size offers ever increasing protection. The analytical model predicts this because, at constant predator density, encounter rates for individual prey with predators are

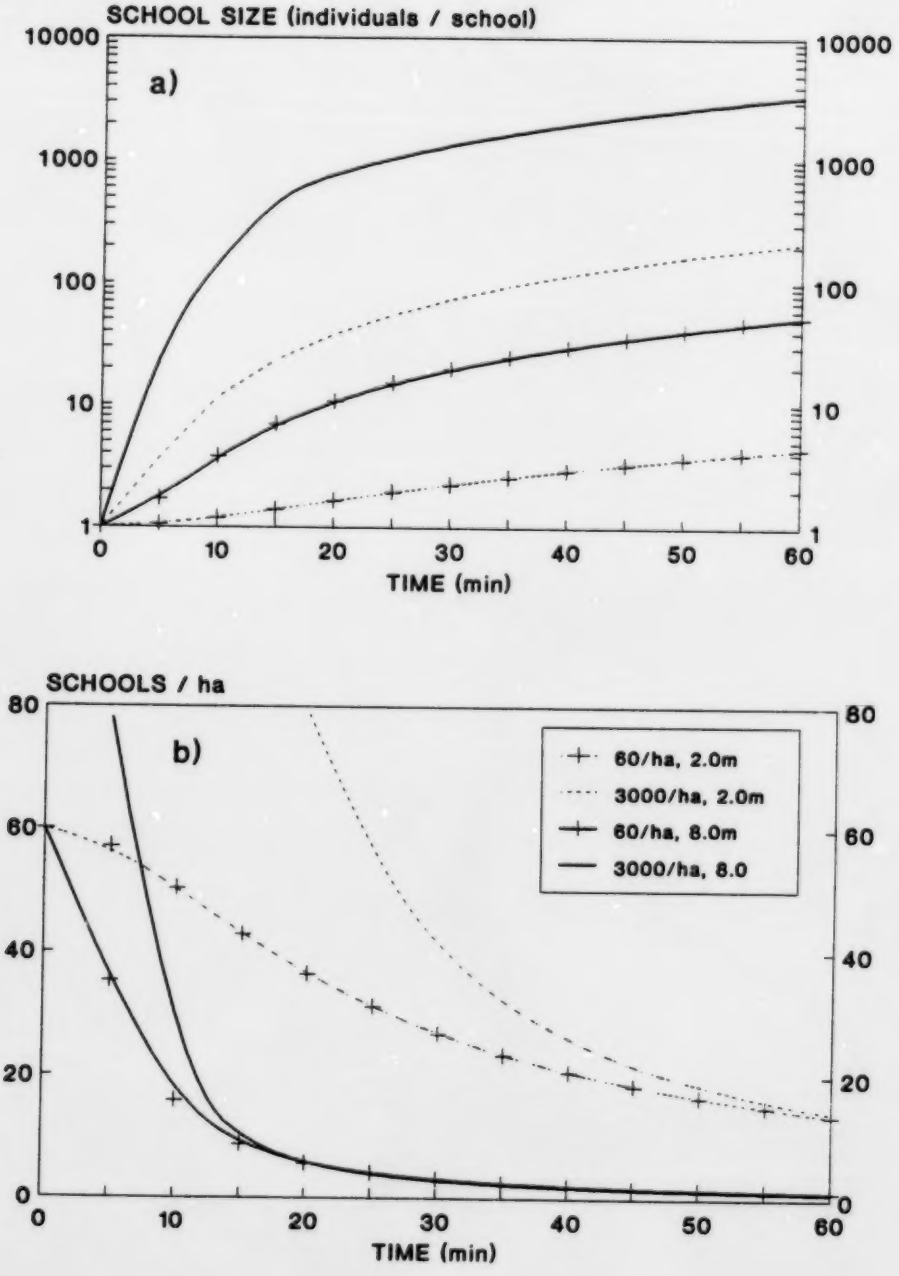

Fig. 2. (a) School size and (b) school density versus time since the initiation of school formation for extreme values of initial density and R_A. Values were produced by the iterative encounter model described in the text.

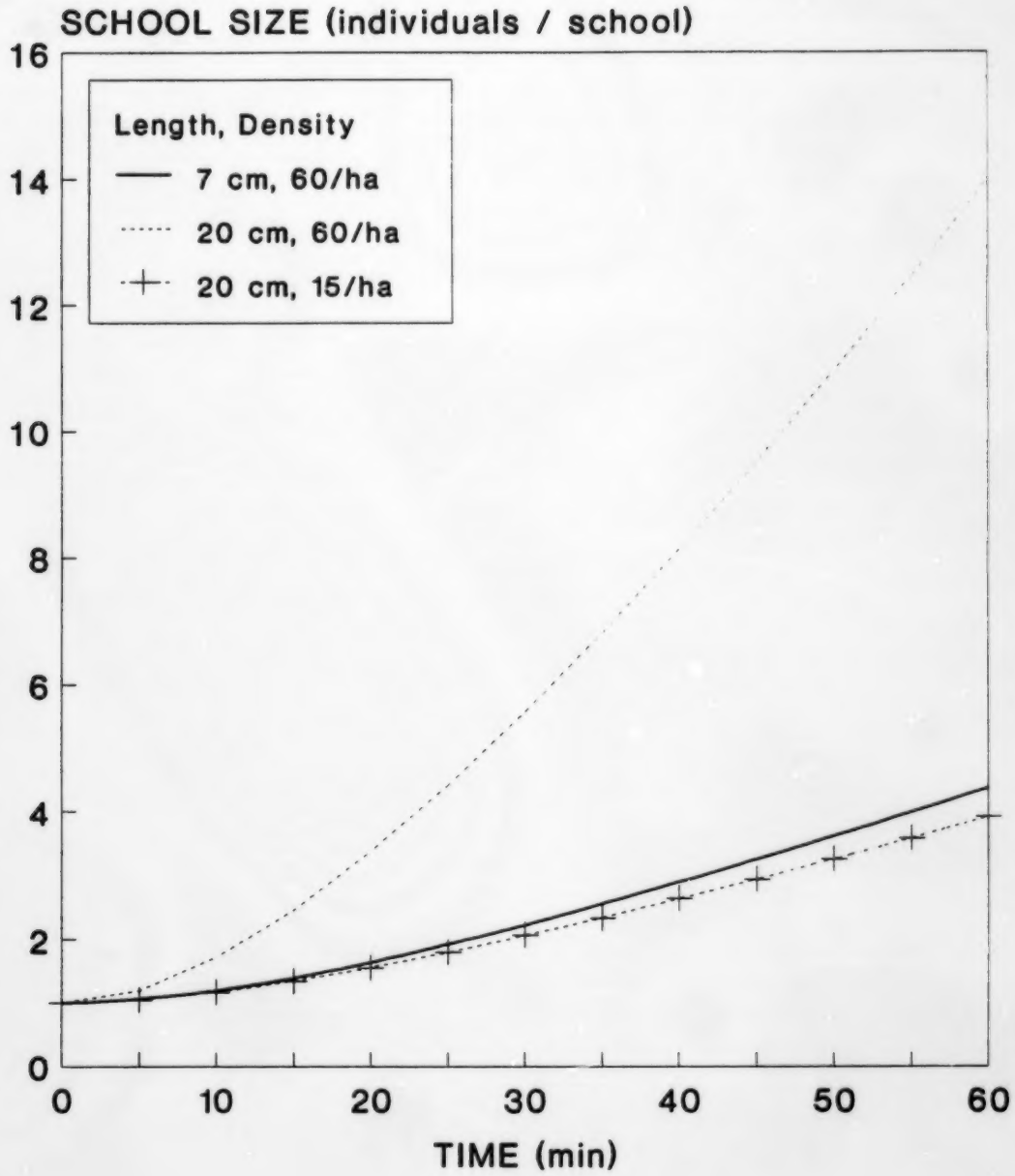

Fig. 3. School size versus time for 7 and 20 cm fish at an initial densities of 60 and 15 fish/hectare. R_A is 2.0 m.

independent of N_H whereas prey encounter rates with prey increase with N_H.

Given enough time, schools can form even at very low densities. Low densities can only result in small schools for a significant length of time if schools form slowly each dawn. The iterative encounter model indicates that, at the high extremes of encounter radius and fish density, that schools of more than 10 fish can form in a few minutes. Conversely, at the low extremes for these parameters prey-prey encounters are so rare that average school size is only slightly over two after 30 minutes. This suggests slow school formation can increase predation risk in the sockeye/kokanee system using realistic parameter values. Direct confirmation of the phenomena is needed, however, since values for encounter radii are poorly defined and a variety of behaviourial modifications could improve school formation at low densities.

A direct estimate of the relationship between rate of school formation and prey density may be possible (using sequential echosounding) and could be used to check the parameters of the model. The model also predicts that, shortly after dawn, school density (schools/hectare) should converge for high and low prey densities.

Aside from these direct predictions, this model also suggests a variety of asymmetries in behaviour between dusk and dawn that result from the prediction that predation risk is higher at dawn and in low density years. Risk of predation is recognized as a powerful modifier of behaviour (Kerfoot and Sih 1987). Since sockeye appear to vertically migrate down, as well as school, to avoid predators during the day (Clarke and Levy, 1988), antipredator behaviourial options for prey include nocturnal aggregation, an earlier and faster search velocity, and an earlier dawn descent. The model suggests that these behaviourial options would be favoured at lower densities and at dawn instead of dusk. Observations of these measurable behaviours under different light and density conditions would help to reveal how both the predators and prey adjust to changes in prey densities. Differences in predation risk and antipredator behaviour may also produce predictable differences in feeding rate between dawn and dusk in both predators and prey. Prey should have fuller stomachs at dusk and dawn/dusk predators should have fuller stomachs at dawn, especially at low prey densities. All of these effects should be exaggerated as encounter radii decline (eg. turbid lakes) but should disappear when encounter radii are very low via a mechanism similar to Clarke and Levy's (1988) antipredation window.

Slight asymmetries of dawn/dusk behaviour have been noted by Helfman (1981) who found that dawn activities take place at lower light levels than the corresponding dusk activities in the

littoral areas of a temperate lake. Attacks of barracuda on silversides in Hawaii peak at twilight but are more frequent at dawn than at dusk particularly in deeper water (Major 1977). Asymmetries in behaviour in pelagic areas should be greater because fish lack a substrate to help them maintain their orientation during the night. In Babine Lake, the dawn depth distribution of sockeye is significantly different than that at dusk (Narver 1970). Sockeye in both Babine Lake (Narver 1970) and Lake Washington (Doble and Eggers 1978) feed more intensely at dusk than at dawn. Sockeye schools in Lake Washington appear to break up at about .17 lux (Eggers 1978) which is above the light level necessary for schooling and feeding in sockeye (Ali 1959). Earlier dawn schooling while feeding is therefore feasible in at least some populations of sockeye.

The problem of ineffective schooling at low densities is part of the more general question of mechanisms for depensatory predation mortality at a given predator density. As discussed by Peterman (1977), one commonly postulated mechanism for depensatory mortality is a Type II or a Type III functional response curve for predators which result from predator satiation at high prey densities. Peterman (1977) argues that, for salmonid predators, a type III (sigmoid) functional response, which produces a predator refuge at low densities, is much more common that a type II response, which produces continually increasing mortality rate at lower densities.

A predation refuge (such as schooling) that is more effective at high densities can modify the effects of these functional response curves. Schools as refuges contrast with physical refuges which are more likely to be already occupied and, if unoccupied, of lower quality at higher densities. If the effectiveness of schools is negligible at very low density and then increases with density, the functional response curve with schooling will initially coincide with the unschooled curve and will then fall away in some manner as schooling begins to inhibit predation. Other examples of predator inhibition at high densities involve social defence (Tostowaryk 1972) and prey disturbance (Mori and Chant 1966). Social inhibition or distasteful prey can produce a type IV functional response curve (Holling 1965) which initially rises and then falls with increasing prey density.

To illustrate the possible effect of schooling, consider the simple case where the natural range of prey density covers only the initial rising leg of a type III functional response curve and the increase in school size with prey density is linear (Fig. 4a,b). The net effect of school formation is that type III curve is converted into a type II functional response curve. Predation mortality decreases continuously with density and catastrophic collapse of prey populations is possible at low density.

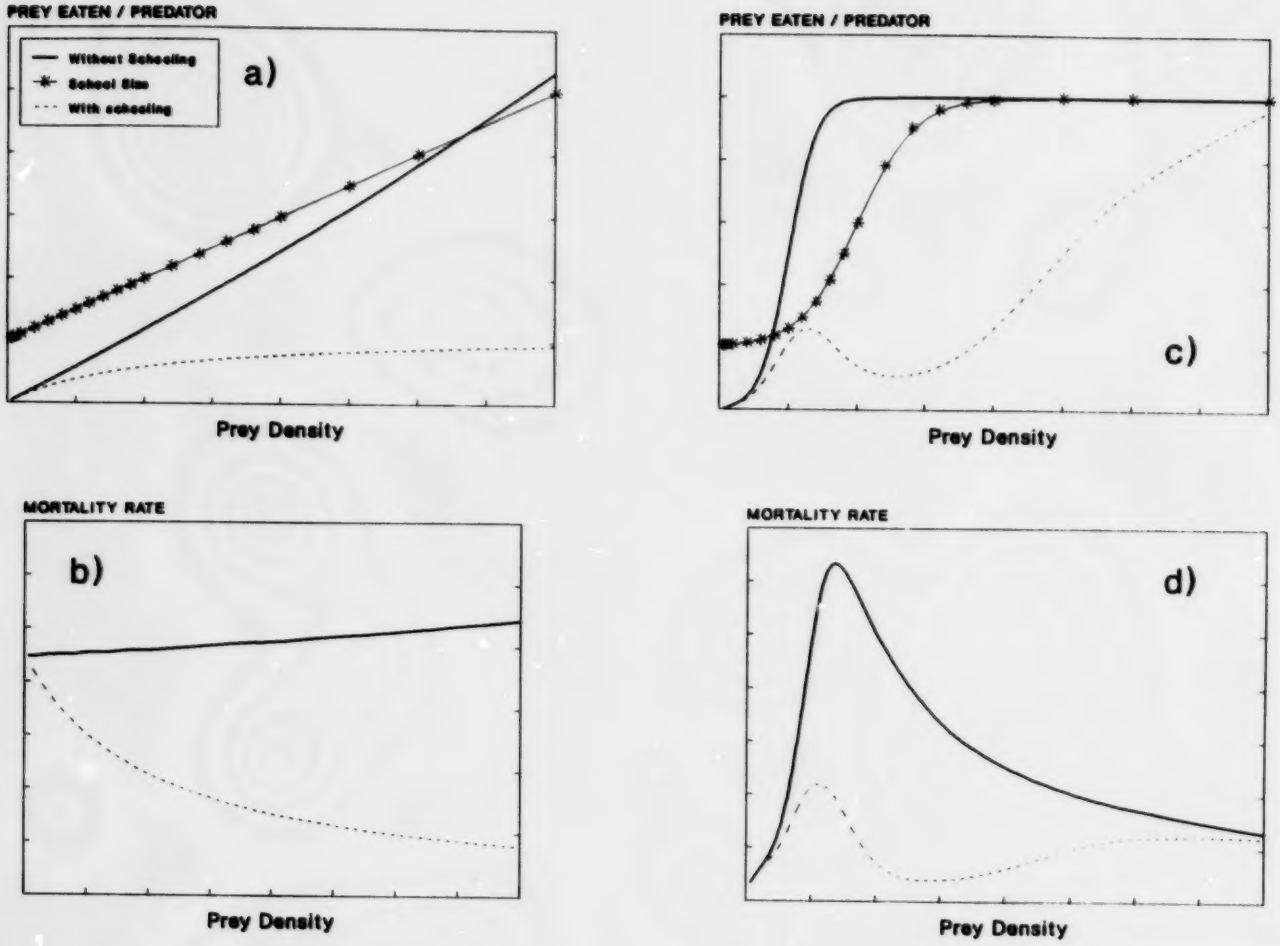

Fig. 4. Possible effects of schooling on the functional response of predators and predation mortality for (a) and (b) the initial portion and (c) and (d) the entire range of a Holling type III functional response curve. For the purpose of this graph, the school size is assumed to have a simple dilution effect, that is, predator consumption per encounter is constant with school size.

Next consider a type III curve where the increase in school size is sigmoid (Fig. 4c,d). In this case, the schooled functional response rises in parallel with the unschooled curve but then breaks away and starts to fall as schooling begins to inhibit predation and finally rises again as the effectiveness of schooling reaches an asymptote. Predation mortality curves with and without schooling both have peaks but the schooled mortality curve has a second rise and predator satiation is not a factor in producing the first peak. Two stable equilibrium prey densities are possible in a situation similar to that described by Peterman (1977) except that both equilibria are predator regulated. A third equilibrium that is not regulated by predators may also exist beyond the second rise in the mortality curve. The initial flat area of the school effect curve could result from the combined effect of small schools that take a long time to form each day. The asymptote could result if there is an optimum school size because of factors such as feeding interference in large schools (Eggers 1976). The functional response curve in Fig. 4c differs from the previously described type IV curve in having a flat beginning and a rising end. Sandness and McMurtry (1970) reported a similar, complex curve for insect predators whose hunting and attack behaviour changed at very high prey densities.

The main point of this discussion is that school formation can result in complex predator functional response curves that produce depensatory mortality in the absence of predator satiation. Over a restricted range of densities, the effects of school formation on prey mortality can be a dominant factor in shaping the functional response curve if large schools are an effective antipredator tactic. A variety of factors interact to determine the shape of the schooling effect curve and the role of schooling in shaping functional response curves will probably have to be determined empirically.

Depensatory predation as a cause of cyclic dominance is a long-standing hypothesis for both sockeye (Ward and Larkin 1964, Larkin 1971) and pink salmon (Ricker 1962), but has been difficult to demonstrate in practice. In at least some pink and chum populations, empirical measurements suggest that predators are operating at the low, linear end of an increasing functional response curve (Peterman and Gatto 1978) but their data is from streams where schools may either be ineffective or form very quickly. Both sockeye fry per predator stomach and the suite of predators seem to increase in Shuswap Lake suggesting that predators are not near the satiation level on their functional response curve (Williams et al. in press). Mortality rates at high densities in Shuswap Lake also appear to be compensatory rather than depensatory (Williams et al. in press). Lack of predator satiation, however, does not rule out school formation as a cause of depensatory mortality at low densities.

Older kokanee may be in an even more vulnerable position than low density sockeye populations since densities of adult kokanee tend to be lower than those of low density underyearling sockeye. In addition, Levy (1989) suggests that older kokanee do not descend during the day and it would therefore appear that schooling is the primary antipredator option open to them. Older kokanee (10-20 cm) are vulnerable to predation and seem to be selected by predators large enough (about three time the length of their prey) to handle them (Parkinson et al., 1989). Predator selection for older, larger kokanee may be partially due to lower school sizes that result from the lower densities of older kokanee. Following a sudden decline in density, older kokanee may face the same density of predators with reduced protection from schooling and few alternative antipredator strategies. Recent collapses of kokanee populations following Mysis introduction (eg. Morgan et al. 1978) may be enhanced by depensatory predation at low densities.

REFERENCES

Ali, M. A. 1959. The ocular structure, retinomotor and photo-behaviourial responses of juvenile Pacific salmon. Canadian Journal of Zoology 37:965-996.

Clarke, C. W. and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist 131: 271-290.

Dunbrack, R. L. and L. M. Dill. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Science 41:1176-1182.

Doble, B. D. and D. M. Eggers. 1978. Diel feeding chronology, rate of gastric evacuation, daily ration and prey selectivity in Lake Washington juvenile sockeye salmon (Oncorhynchus nerka). Trans. Am. Fish. Soc. 107:36-45.

Eggers, D.M. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. Journal of the Fisheries Research Board of Canada 33:1964-1971.

Eggers, D.M. 1978. Limnetic feeding behaviour of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnology and Oceanography 23:1114-1125.

Gerritsen, J. and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Research Board of Canada 34:73-82.

Glass, C. W. and C. S. Wardle. 1989. Comparison of the reactions of fish to a trawl gear at high and low light intensities. Fish. Res. 7:249-266.

Glass, C. W., C. S. Wardle and W. R. Mojsiewicz. 1986. A light intensity theshold for schooling in the Atlantic Mackerel, Scomber scombrus. J. Fish. Biol. 29 (Supp. A):71-81.

Godin, J. G. J. 1986. Antipredator function of shoaling in teleost fishes: A selective review. Naturaliste Canadienne 113:241-250.

Helfman, G. S. 1981. Twilight activities and temporal structure in a freshwater fish community. Canadian Journal of Fisheries and Aquatic Sciences 38:1405-1420.

Helfman, G. S. 1986. Fish behaviour by day, night and twilight. p. 366-387. In T. J. Pitcher (ed.), The behaviour of teleost fishes. Croom Helm, London, England.

Henderson, M. A. and T. G. Northcote. 1985. Visual prey detection and foraging in sympatric cutthroat trout (Salmo clarki clarki) and dolly varden (Salvelinus malma). Canadian Journal of Fisheries and Aquatic Sciences 42:785-790.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada 45:5-61.

Kerfoot, W. C. and A. Sih. 1987. Predation. New England University Press, Hanover, New Hampshire, U.S.A.

Larkin, P. A. 1971. Simulation studies of the Adams River sockeye salmon (Oncorhynchus nerka). Journal of the Fisheries Research Board of Canada 28:1493-1502.

Levy, D. A. 1987. Review of the ecological significance of diel vertical migrations by juvenile sockeye salmon (Oncorhynchus nerka). P. 44-52. In H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (Oncorhynchus nerka) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96.

Levy, D. A. 1989. The selective advantage of diel vertical migration behaviour in juvenile sockeye salmon and kokanee (Oncorhynchus nerka). Ph.D. thesis, Univ. of B. C., Vancouver, B.C. 123 p.

Major, P. F. 1977. Predator-prey interactions in schooling fishes during periods of twilight: A study of the silverside Pranesus insularum in Hawaii. Fisheries Bulletin 75:415-426.

Major, P. F. 1978. Predator-prey interactions in two schooling fishes, Caranx ignobilis and Stolephorus purpureus. Animal Behaviour 26:760-777.

Morgan, M. D., S. T. Threlkeld, and C. R. Goldman. 1978. Impact of the introduction of kokanee (Oncorhynchus nerka) and opossum shrimp (Mysis relicta) on a subalpine lake. Journal of the Fisheries Research Board of Canada 35:1572-1579.

Mori, H. and D. A. Chant. 1966. The influence of prey density, relative humidity, and starvation on the predacious behaviour of Phytoseiulus persimilis Anthias-Henriot (Acarina: Phytoseiidae). Canadian Journal of Zoology 44:483-491.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye and the limnetic zooplankton in Babine Lake, British Columbia. Journal of the Fisheries Research Board of Canada 27:281-316.

Parkinson, E. A., J. M. B. Hume and R. Dollighan. 1989. Size selective predation by rainbow trout on two lacustrine Oncorhynchus nerka populations. B. C. Fisheries Branch, Fisheries Management Report 94, 14p.

Peterman, R. M. 1977. A simple mechanism that causes collapsing stability region in exploited salmonid populations. Journal of the Fisheries Research Board of Canada 34:1130-1142.

Peterman, R. M. and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. Journal of the Fisheries Research Board of Canada 35:797-808.

Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. p. 294-337. In T. J. Pitcher (ed.), The behaviour of teleost fishes. Croom Helm, London, England.

Pitcher, T. J. and J. R. Turner. 1986. Danger at dawn: experimental support for the twilight hypothesis in shoaling minnows. Journal of Fish Biology 29 (Supp. A):59-70.

Ricker, W. E. 1962. Regulation of the abundance of pink salmon populations, p. 155-211. In N. J. Wilimovsky (ed.) Symposium on Pink Salmon. Institute of Fisheries, Univ. of B. C., Vancouver, B. C.

Sandness, J. N. and J. A. McMurtry. 1970. Functional response of three species of Phytoseiidae (Acarina) to prey density. Canadian Entomology 102: 692-704.

Tostowaryk, W. 1972. The effect of prey defense on the functional response of Podisus modestus (Hemiptera: Pentatomidae) to densities of the sawflies Neodiprion swainei and N. pratti banksianae (Hymenoptera: Neodiprionidae). Canadian Entomology 104:61-69.

Van Olst, J. C. and J. R. Hunter. 1970. Some aspects of the organization of fish schools. Journal of the Fisheries Research Board of Canada 27:1225-1238.

Vermeij, G. J. 1982. Unsuccessful predation and evolution. American Naturalist 120:701-720.

Vinyard G. L. and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal of the Fisheries Research Board of Canada 33:2845-2849.

Ward, F. J. and P. A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. International Pacific Salmon Fisheries Commission Progress Report 11, 116 p.

Ware, D. M. 1973. Risk of epibenthic prey to predation by rainbow trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 30:787-797.

Ware, D. M. 1978. Bioenergetics of pelagic fish: Theoretical change in swimming speed and ration with body size. Journal of the Fisheries Research Board of Canada 35:220-228.

Williams, I. V., D. Brock, P. Gilhousen. T. Gjernes, K. Morton, R. Johnson and W. Saito. (in press). Studies of the lacustrine biology of the sockeye salmon (Oncorhynchus nerka) in the Shuswap system. International Pacific Salmon Fisheries Commission Report.